Chapter 3
Soil Organisms and Ecological Processes

Abstract Previously, the soil ecosystem acting as habitat and food resource for soil organisms and the living soil and its wide variety of groups were introduced. This chapter will introduce the functional role of soil organisms on significant ecological processes, such as soil nutrient availability, biological control, soil structure, herbivory, symbiosis, and plant growth. Ecosystem engineers, litter transformers, predators, herbivores, symbionts, microregulators, decomposers, and prokaryotic transformers are essential for the soil ecosystem functioning because they promote services that provide habitat and food resource for the entire soil food web (e.g., including the primary producers). Basically, soil organisms are living individuals which live into soil ecosystem (e.g., by creating nests and galleries), and they have key role in increasing nutrient cycling, plant growth, soil structure, and plant resistance to abiotic and biotic stresses in tropical ecosystems. They can increase plant growth (e.g., by symbiotic relationships helping plants to uptake N, P, and micronutrients), litter deposition (e.g., by increasing the production of phytohormones to start leaf senescence processes), nutrient cycling (e.g., by increasing litter transformation and soil organic matter decomposition), and soil food web (e.g., by promoting a wide range of functional groups, and controlling the dominance of potential pathogen groups).

Keywords Biological control promoted by soil organisms · Plant growth · Symbionts in tropical ecosystems · Soil nutrient availability · Structuring soil profiles

Questions Covered in the Chapter

1. How do soil organisms affect important ecological processes into soil ecosystem?
2. How do litter transformers and decomposers promote soil nutrient availability?
3. How do microregulators and predators promote biological control?
4. How do ecosystem engineers promote soil structure?
5. How do symbionts help plants to uptake water and nutrients?
6. How does plant growth could be promoted by soil organism activity?

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3.1 Introduction

Soil organisms (hereafter soil biota) are living individuals for a wide range of groups that are present into soil profile, and in tropical ecosystem, they play a role in providing important ecosystem services (Li et al. 2021). They can do the following:

1. Transform and incorporate the litter and other organic compounds that were deposited on soil surface thus having an important role in nutrient cycling.
2. Control population picks into their own community thus avoiding overpressure.
3. Make complex structures inside soil profile thus facilitating water movement and root growth.
4. Produce volatile compound that attracts herbivores and predators thus controlling leaf transpiration, photosynthetic rate, primary production, and herbivory pressure. At the tropics, in natural semiarid ecosystem, this process plays a key role on environmental sustainability.
5. Colonize plant roots thus promoting water and nutrient uptake.
6. Promote plant growth through biotic stresses thus stimulating phytohormone production, such as plant defensive response against herbivore insects.

Overall, soil organisms control litter deposition rate, soil organic matter transformation, plant mineral nutrition, and biological control (Andrea et al. 2018; Rodriguez et al. 2021;), increasing mineral nutrient availability (e.g., N, P, K, and micronutrients), plant growth (e.g., above- and belowground biomass production), and resistance tolerance to abiotic and biotic stresses in tropical conditions (Majeed et al. 2018; Yang et al. 2018). We can find soil organisms acting in several habitats into tropical ecosystems, such as forests, grasslands, shrublands, scrublands, and highly anthropogenized habitats. As they consist of a wide range of groups varying in their behavior, habitats, and food preferences, they exhibit different community composition, and it is dependent of plant community diversity, soil contents of C and N, and climate attributes (Zhang et al. 2017; Sprunger et al. 2019; Heydari et al. 2020). Some soil organism groups are dominant into soil profile (ecosystem engineers), like Blattidae, Formicidae, and Termitidae (Tuma et al. 2019a; Franco et al. 2020; Lavelle et al. 2020), but there are fewer dominant groups that play important functions (litter transformers and predators), like Scarabaeidae, Scutigeromorpha, and some soil nematodes (Liu et al. 2019; Gonçalves et al. 2021). Many works have also suggested that soil organisms may exhibit different distribution patterns and functional redundancy resulting in a high variability of diversity and composition between land uses or natural ecosystems (Silva et al. 2017; Potatov et al. 2019; Kooch et al. 2020).

3.2 Soil Nutrient Availability

Soil organisms are strongly dependent to C and N sources on soil profile, being unable to act improving soil ecosystem if these two nutrients were unavailable or in low contents (Potatov et al. 2017; Lin et al. 2017). Usually, in tropical ecosystems with high provision of habitat and food resources, soil organisms improve soil nutrient availability following three distinct pathways (Fig. 3.1).

They start degrading whole litter material by physical trituration (Joly et al. 2020; Brosseau et al. 2019) through their mouthparts (e.g., litter transformers are characterized by presenting a robust pair of mandibles). Next, they carry litter residues into soil profile by bioturbation process (Sofo et al. 2020a; McCary and Schimitz 2021). Here, litter transformers promote soil excavation, seed exhumation (e.g., by improving soil seed bank viability), and L-layer formation and provide habitat to generalist decomposers (e.g., yeast) which in turn start degrading litter residues by enzymatic activity (Urrea-Galeano et al. 2019; Lucena et al. 2021). One important point during this process is that we can split soil mineral phase from litter residues. Finally, once the soil organic matter has been produced, only specialist decomposers act promoting decomposition (e.g., mineralization and humification) and nutrient cycling process (López-Mondéjar et al. 2018; Brunel et al. 2020; Husson et al. 2021). This final pathway occurs exclusively through chemical alteration promoted by microbial enzymes (Table 3.1).

3.3 Herbivory

Probably, the interaction between plant and soil organisms classified as herbivores (e.g., arthropods and nematodes) is the most ancient ecological interaction in the humankind history (Currano et al. 2021). During this process, the soil organisms feed several parts of the plant (e.g., leaves, roots, branches, flowers, fruits, and seeds) thus releasing chemical signals that induce plants to start their defense response (Yang et al. 2021). Here, it is important to know that the herbivory is an important and natural process that occurs all the time around all the world. Into this context, it is incorrect to classify a herbivore as a "pest" (Heinze 2020). In natural conditions where there is a complex habitat with a high diversity of plant species, the herbivory is beneficial for the plant species (Cortois et al. 2017; Wan et al. 2020b). It helps the plant species into four different ways:

1. It reduces plant transpiratory rate by reducing the leaf area. It is so necessary into semiarid ecoregions where there is a long dry period.
2. It acts as an "enzyme" catalyzing the leaf senescence stage thus promoting the litter deposition.
3. It enables the plant species to produce phytohormones and pigments that attract predators thus promoting biological control.
4. Leaf-feeders can promote pollination by transporting pollen.

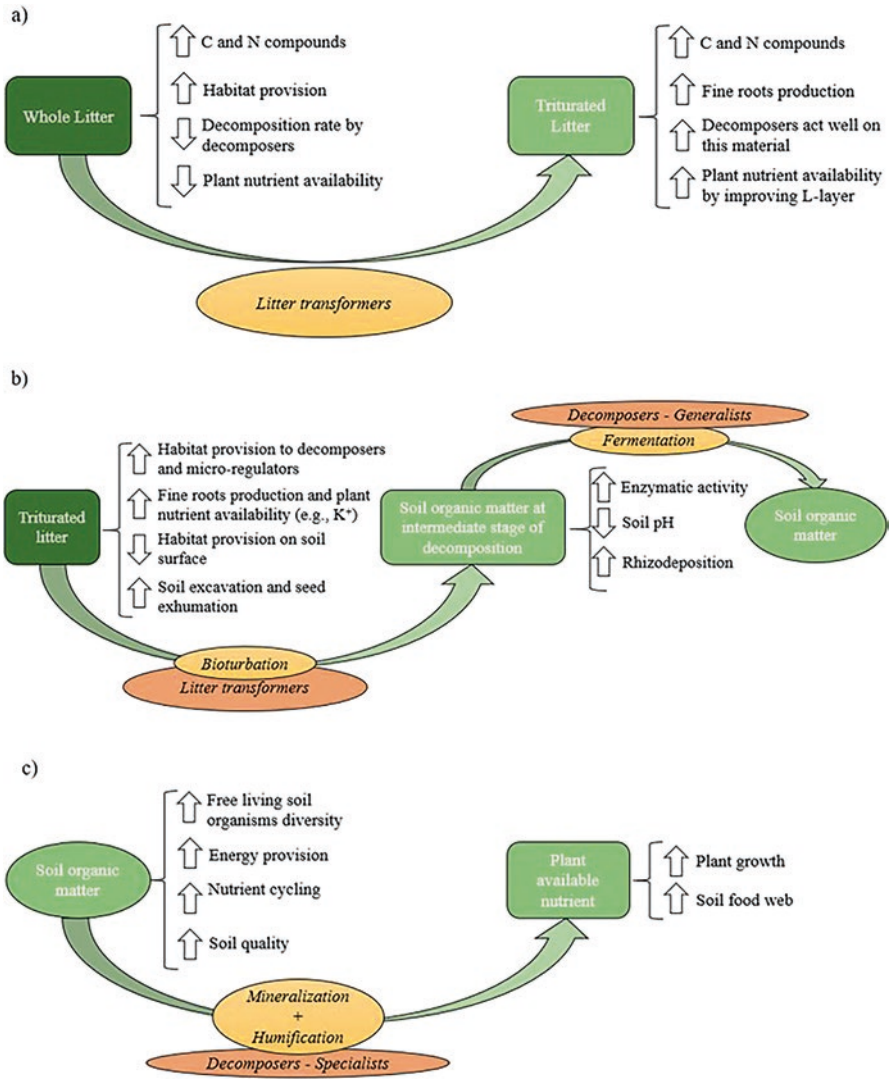

Fig. 3.1 Schematic view showing how do litter transformers and decomposers promote soil nutrient availability in tropical ecosystems: (**a**) physical pathway (litter trituration), (**b**) physical-chemical pathway, and (**c**) chemical pathway (enzymes). (Adapted from Wutzler et al. (2017), Magcale-Macandog et al. (2018), Griffiths et al. (2021), Homet et al. (2021))

However, in tropical agriculture where the natural ecosystem is simplified into monocropping systems, the herbivore pressure on annual plant species is too high because of the reduction of plant diversity, habitat provision, and food availability. Thus, creating a negative feedback and a hard scenario where the herbivores impose

Table 3.1 Main enzymes produced by decomposers

Enzyme	Action
Amidase	It catalyzes the breakdown of N-rich organic compounds into ammonium NH_4
Amylase	It catalyzes the breakdown of starch into sugar
Aminoacylase	It catalyzes the N-acyl-L-amino acid into carboxylate and L-amino acid
Aminopeptidase	It catalyzes the cleavage of amino acids into proteins or exopeptidases
Asparaginase	It catalyzes the breakdown of asparagine into ammonia and aspartic acid
Catalase	It catalyzes the hydrogen peroxide into water and oxygen
Cellulase	It catalyzes the cellulose molecule into monosaccharides
Cutinase	It catalyzes the breakdown of cutin into cutin monomers
FDA hydrolysis	It catalyzes the decomposition of soil organic matter into glucose
Galactosidase	It catalyzes the hydrolysis of galactosides into monosaccharides
Glucosidase	It catalyzes the breakdown of carbohydrates into glucose
Glucose isomerase	It catalyzes the interconversion of D-xylose and D-xylulose
Glucose oxidase	It catalyzes the glucose into hydrogen peroxide and D-glucono-δ-lactone
Glucoamylase	It catalyzes the alpha-D-glucose residues into beta-D-glucose
Invertase	It catalyzes the breakdown of sucrose into fructose and glucose
Laccase	It oxidizes a variety of phenolic substrates, such as lignin
Lactase	It catalyzes hydrolysis of the lactose into galactose and glucose monomers
Lipase	It catalyzes the breakdown or hydrolysis of fats
Oxygenase	It oxidizes a substrate by transferring the oxygen from O_2 to it
Pectinase	It catalyzes the breakdown of pectin
Phosphatase	It catalyzes the breakdown of inorganic P into phosphate
Protease/ Proteinase	It catalyzes the breakdown of proteins into smaller polypeptides
Phytase	It catalyzes the hydrolysis of phytic acid into inorganic phosphorus
Sulfatase	It catalyzes the breakdown of sulfur into sulfate
Urease	It catalyzes the breakdown of urea into ammonia and carbon dioxide
Transglutaminase	It catalyzes the formation of an isopeptide bond between glutamine residue and lysine residue with subsequent release of ammonia
Tyrosinase	It catalyzes the oxidation of phenols such as tyrosine and dopamine using dioxygen
Xylanase	It catalyzes the breakdown of linear polysaccharide xylan into xylose

Adapted from Ba and Kumar (2017), Garske et al. (2017), Ren et al. (2017), Dotaniya et al. (2019); Gunjal et al. (2019), Lincoln et al. (2019), Sorde and Ananthanarayan (2019), Shi et al. (2019), Unuofin et al. (2019), Hou et al. (2020), Norman et al. (2020), Vara and Karnena (2020), Wan et al. (2020a), Wilkerson and Olapade (2020), Ivaldi et al. (2021)

a stress that annual plant species have no conditions to resist by their own (Bennett and Klironomos 2018). In general, we can find two situations regarding the herbivory into the tropics: a positive and a negative feedback related to natural ecosystem and monocropping system, respectively (Fig. 3.2).

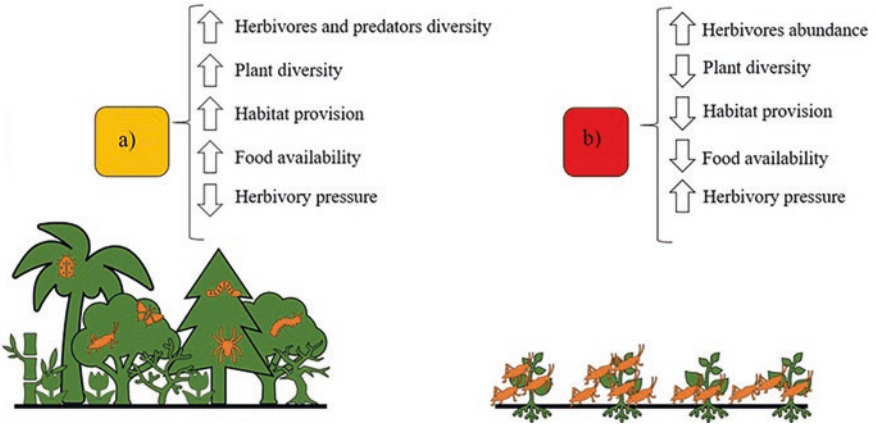

Fig. 3.2 Schematic view showing how do herbivores and plant species interact in (**a**) natural ecosystem and (**b**) monocropping system. (Adapted from Yang et al. (2018), Bennett et al. (2019), Wan et al. (2019))

3.4 Biological Control

It is another natural ecological process that occurs into soil ecosystem constantly, but it is extremely sensitive to changes and disturbances both at temporal and spatial scale (Neher and Barbercheck 2019). We can define the biological control into the tropical soils as the sum of predators and microregulators activity (Marsden et al. 2020). Here, predators (e.g., Chilopoda, Dermaptera, Mantodea, Scorpiones, and some families from Coleoptera) act as controlling agent in the population of individuals from macrofauna and mesofauna groups, especially herbivores, while microregulators (e.g., Acari, Collembola, some carnivores Nematodes, and other microorganisms) act as controlling agents in microbiota population into soil profile and around the rhizosphere microbiome (Lazarova et al. 2021). Because of this process in natural ecosystem, we never find high herbivory pressure or high abundance of a specific group (e.g., high abundance of larvae of Coleoptera) at the tropics (Ciancio and Gamboni 2017; Sankaranarayanan et al. 2019). Here, it is important to clarify the difference between the idea of dominance and abundance into soil ecology (Arnan et al. 2018). Even in natural ecosystem, we can naturally find dominant groups such as ecosystem engineers (e.g., Formicidae and Termitidae), and it does not reflect a disturbance or a negative feedback (Tuma et al. 2019b; Vanolli et al. 2021). It is a natural phenomenon following the biology and behavior of ants and termites to live into colonies (Menzel and Feldmeyer 2021). On the other hand, abundance reflects the number of a specific taxon for an area or a specific ecosystem (de Cristo et al. 2019). High abundance rates for a specific taxon, i.e., herbivores from Cerambycidae and Hemiptera and larvae of Lepidoptera, Orthoptera, or Phasmatodea, could reflect disturbance, reduction into plant diversity, and low predator abundance. In this context, we can find a reduction on the biological control,

such as in the case of tropical monocropping systems where there is a high herbivory pressure promoted by the reduction of food availability and habitat provision that in turn leads to a drastic reduction on predator abundance (Dietrich et al. 2021).

3.5 Soil Structure

Ecosystem engineers (e.g., ants, cockroaches, earthworms, isopods, and termites) affect soil structure by promoting bioturbation and physical alteration of the organic matter (e.g., consumption of litter and production of fecal pellets) and building physical structures in soil profile that act as habitat for decomposers and prokaryotic transformers (Piron et al. 2017; Jouquet et al. 2018; Domínguez et al. 2018; Sagi and Hawlena 2021). During bioturbation, soil organisms promote the movement of materials through soil surface and soil profile. Litter transformers promoted soil excavation, litter incorporation (e.g., contributing to O horizon formation), seeds dispersion and exhumation (McTavish and Murphy 2021; Wiesmeier et al. 2019). In soil profile, they consume organic detritus and produce fecal pellets. These pellets provide a favorable habitat to decomposers, thus increasing decomposition rate and nutrient release (Sagi et al. 2021). Finally, soil engineers create a complex chain of channels because of their activity. It positively modifies the soil macropores (e.g., also classified as biopores), soil porosity, and drainage (Lehmann et al. 2017). One important point into this process is that all activities are exclusively promoted by soil organisms from macrofauna group (Gongalsky 2021).

3.6 Symbiosis

Some individuals in Fungi and Bacteria groups (e.g., arbuscular mycorrhizal fungi and N-fixing bacteria) can establish a symbiotic relationship with plant species (Porter and Sachs 2020). These microorganisms are present in all tropical ecosystems and have an important role in both plant mineral nutrition (e.g., N, P, and micronutrient uptake) and water absorption (Winagraski et al. 2019; Medeiros et al. 2021). They produce structures inside roots (e.g., arbuscules for fungi from Phylum Glomeromycota and nodules for bacteria from Family Rhizobiaceae) (Uroz et al. 2019) that act as a specialized tool for the exchange of nutrients between the symbionts (Jacott et al. 2017). The AMF symbiosis results in increased plant growth, resistance, and tolerance to abiotic and biotic stresses (Naik et al. 2019). After primary production (Fig. 3.3), the symbiosis is the second basis of the soil food web (Antunes and Koyama 2017).

Into Glomeromycota, the arbuscules are originated among the cell wall and plasma membrane of root cortical cells by differentiating the intracellular hyphae (Souza 2015), while into Rhizobiaceae, the nodules are originated by creating a pathway for the bacterial cell to travel inside the root epidermal cells

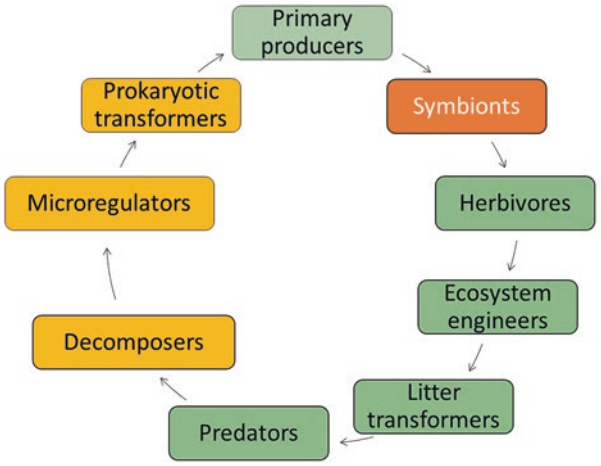

Fig. 3.3 Schematic view of the entire soil food web. (Adapted from Veldhuis et al. (2018))

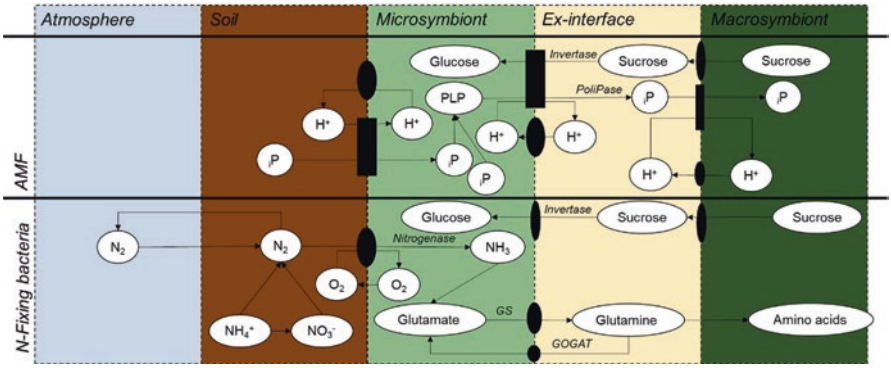

Fig. 3.4 Main events of the symbiotic process following the pathways for an arbuscular mycorrhizal fungus (AMF) and a nitrogen fixing (N-fixing) bacteria. (Adapted from Chang et al. (2017), Meng et al. (2018))

(Gaudioso-Pedraza et al. 2018). The nodulation begins when the nod factor initiates root hair curling around the bacterial cell (Zanetti et al. 2020). Here, we must consider that the symbiotic relationship is modulated by specific genes thus creating different levels of host specificity during symbiont pairing (Andrews et al. 2018; Kimeklis et al. 2019). Also, we can find some plant species that present inside their roots both fungi and bacteria acting as symbionts. This phenomenon is called tripartite symbiosis and occurs most frequently in legumes (Wang et al. 2021).

In general, the main function of the symbiosis is to provide for the host-plant essential nutrients through its colonized roots (Ingraffia et al. 2019). Even the function being the same, fungi and bacteria (e.g., arbuscular mycorrhizal fungi and N-fixing bacteria) exchange nutrients in totally different pathways (Fig. 3.4).

Arbuscular mycorrhizal fungi provide nutrients, i.e., in general inorganic P ($_i$P), but they can also provide other macro- and micronutrients, for the host plant, which in turn provide to the fungus C-rich compounds (e.g., glucose) (Lanfranco et al. 2019). Here the nutrient exchange is modulated by H+ extrusion at soil-microsymbiont, microsymbiont-exchange-interface, and exchange-interface-macrosymbiont zones (da Silva et al. 2021), thus being extremely sensitive to changes in soil pH (See H^+ extrusion hypothesis proposed by Ramos et al. 2009) and dependent to a specific enzyme (e.g., PoliPase) that breaks down the polyphosphate molecule into single iP at exchange interface zone (Lorenzo-Orts et al. 2019; Recorbet et al. 2021). For the N-fixing bacteria, the symbiotic process occurs totally different from the AMF pathway (Foo 2019; Sakamoto et al. 2019). Here, the bacteria need an aerobic condition (e.g., the presence of dissolved O_2 into soil solution) (García-Cabrera et al. 2020; Rutten and Poole 2019; Verma et al. 2020). It activates the nitrogenase enzyme at the microsymbiont structure (e.g., root nodules), thus being extremely sensitive to changes in soil aeration and soil water regime (Nishida and Suzaki 2018; Schwember et al. 2019; Rutten et al. 2021). Other three enzymes work into this pathway, i.e., invertase by converting sucrose into glucose, *GS* by converting glutamate into glutamine, and finally GOGAT by converting glutamine into glutamate, thus controlling the biological fixation of N and plant uptake (Santos et al. 2018; Fonseca-García et al. 2021).

3.7 Plant Growth

As already shown, all the previous processes can directly and indirectly promote plant growth (Souza and Santos 2018; Lekberg et al. 2018). However, our focus here will be on mineralization that is governed by decomposers and prokaryotic transformers (Hellequin et al. 2018; Suleiman et al. 2019). In general, there are three main pathways that both decomposers and prokaryotic transformers can affect nutrient mineralization:

1. Selective feeding on microbiota: Promoted by selective soil organisms (e.g., fungivores and bacterivores) that choose to feed particular individuals from microbiota group over others. It can lead to positive changes in soil-plant feedback and has a dramatic effect on prey's activity as described by the "*knock-on*" (Iordache 2020).
2. Altering the soil organic matter forms (e.g., litter, F, and H layers): microbial-feeding fauna enhances C and N mineralization that resulted from increased turnover rate and microbial activity (e.g., respiration) and from the excretion of excessive N on microbial cell, respectively (Thakur and Geisen 2019; Sofo et al. 2020b).
3. Hormonal effects on root morphology: Also described as a non-nutritional effect, it is played by protozoa, some nematodes, and other bacteria taxa that influence plant species to produce growth-promoting hormones (e.g., auxins) through their

activity near the rhizosphere (Keswani et al. 2020) thus promoting changes in root architecture (e.g., plant species developing a highly branched root system) (Bavaresco et al. 2020; Pan et al. 2020; Lynch et al. 2021).

3.8 Conclusions

Soil organisms promote important service in the ecosystem processes of soil nutrient availability, biological control, soil structure, herbivory, symbiosis, and plant growth. They are essential for the soil ecosystem functioning because they promote services that provide habitat and food resource for the entire soil food web (e.g., including the primary producers). They promote plant growth (e.g., by symbiotic relationships helping plants to uptake N, P, and micronutrients), litter deposition (e.g., by increasing the production of phytohormones to start leaf senescence processes), nutrient cycling (e.g., by increasing litter transformation and soil organic matter decomposition), and soil food web (e.g., by promoting a wide range of functional groups and controlling the dominance of potential pathogen groups). However, even knowing all these processes, we must consider that they occur simultaneously interacting with each other that has cascading effects on soil food web. As already described, soil organisms can influence soil structure, nutrient availability, and primary production (e.g., measured by the plant growth), thereby affecting the habitat provision and the food availability to the entire soil food web.

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